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COMPARATIVE MORPHOLOGY AND PHYSIOLOGY OF THE CHEMO- AND PRESSORECEPTORS OF THE CAROTID ARTERIES AND THE AORTA

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Introduction

For a long time it has been believed that regulation of respiration, blood pressure, and heart rate in the vertebrates depended entirely upon direct stimulation of centers in the medulla, the respiratory, vasomotor, and cardiac centers respectively. Recently, however, it has been shown that regulation of these very vital processes depends in part upon reflexes arising in the epithelial bodies, located in and around the carotid and aortic arteries. They are referred to as chemo or pressoreceptors depending upon whether they are stimulated by changes either in the chemical content or in the pressure of the blood.

Pressoreceptors

Ask Upmark (1935) presented a short history of the carotid pressoreceptors, which I shall review briefly. As early as 1811 a slight bulb-like dilatation was noticed by Burns at the base of the internal carotid artery. At that time it had been referred to as a pathological condition representing a state of insanity (Meyer, 1877). Later, as the dilation was noticed in all cases examined, it was no longer believed to be a pathological condition, but a normal condition representing the rest of the third branchial artery, from which the carotid artery is derived (Schaffer, 1877). Tandler (1902) suggested that it represented a stage in the development of the internal carotid artery. It was not until

1924, however, that the physiological significance of the body was known. By exerting pressure in the neck region, or by pulling the internal carotid heartward, many investigators have obtained a drop in blood pressure (Parry, 1799; Sir Astley Cooper, 1836; Waller, 1862; Knoll, Czermak, 1880; Sollman & Brown, 1912; Enderle, 1924; Tillman, 1924). This phenomenon was first believed to be due to direct stimulation of the centers in the medulla (Francois Frank, 1880). Hunt (1899) explained it on the basis of inhibition of vagal tone. Hering (1924), however, pointed out that this response depended upon a reflex action originating in the carotid sinus.

Other areas sensitive to changes in pressure have also been found. They include endings on the right subclavian artery, on the arch of the aorta, and on the base of the left subclavian artery (Anrep and Segall, 1926; Lutz, 1930; Koniadez, 1935).

Chemoreceptors

A structure referred to as the carotid body was found in the angle between the internal and external carotid arteries (Haller, 1743, quoted by Boyd, 1937). At that time it was believed to function as an endocrine organ. Even as late as 1933 a substance antagonistic to adrenalin was extracted from the carotid gland or body of Elasmobranchs (Christie). Dreuner (1924, quoted by Ask Upmark, 1935) suggested that the

carotid body represented a sensory organ. Other investigators confirmed the statement (De Castro, 1926; Jacobovici, Nitescu and Pop, 1928; Schmidt, 1932, Heymans, Bouckaert and Dautrebande, 1931; Nonidez, 1935). Heymans, Bouckaert and Dautrebande (1931) showed that the denervation of the carotid sinus at the level of the bifurcation will destroy its sensitivity to pressure changes but not to changes in the gaseous content of the blood; while denervation one-half to one centimeter higher abolishes the sensitivity to both. This occurs since the branch to the carotid body leaves the carotid sinus nerve one-half to one centimeter craniad to the carotid sinus. Other structures also believed to be chemoreceptors have recently been found above the arch of the aorta and below the arch of the aorta just above the ductus arteriosus, (Anrep and Segall, 1926; Palme, Penitschka, 1934, quoted by Nonidez, 1935; Muratori, 1934; Nonidez, 1935, 1937).

There will be an attempt made in this paper to compare both morphologically and physiologically these various bodies in the different classes of vertebrates.

Derivatives of the Aortic Arches

Since the epithelial bodies represent integral parts of the aortic arches, and since they are derivatives of the primitive branchial arches found in the fishes, a knowledge of the evolution of the aortic arches is of utmost importance. In the fishes there are usually six branchial arches which

connect the dorsal with the ventral aorta after ramifying through the gills. Very early in the development, the first two aortic arches lose their respiratory function and consequently no longer persist as aortic arches. In Anura the third, fourth and sixth aortic arches persist. The ductus Botalli between the pulmonary artery and the dorsal aorta disappears. The third, fourth, and sixth aortic arches continue to remain, even in the mammals. The right portion of the fourth arch forms the right subclavian artery; whereas the left part becomes the left aortic arch. The third arch of the embryo gives rise to the common carotid. The pulmonary artery is derived from the sixth arch (Neal and Rand, 1936).

The carotid sinus and carotid body are derivatives of the third branchial arch; the pressoreceptor endings on the right subclavian artery, on the arch of the aorta, and in the aortic body, together with the chemoreceptor endings in the paraganglion supracardiale superius and inferius are derivatives of the fourth arch, and the paraganglion supracardiale aorticum is a derivative of the sixth arch.

Part I Pressoreceptors

The pressoreceptors are afferent nerve endings present in the carotid sinus, on the right subclavian artery, on the arch of the aorta and the base of the left subclavian. These nerve endings are generally arranged in a periglandular, an interstitial and a periglomerular plexus. The detailed structure of the pressoreceptors, however, varies with the

form of the vertebrate studied. Changes in pressure, bringing about a distension of the wall of the sinus or artery, constitute the normal physiological stimuli. The degree of the response is directly proportional to the amount of distension and is always the same for the same amount of distension (Tournade et G. Dubreuil, 1932). The responses brought about are vaso-dilation, decrease in heart rate and respiration. Changes in the respiratory gases in the blood also influence their activity to a slight extent. Increase in the oxygen content increases their activity; whereas an increase in the carbon dioxide content decreases their activity (Marie and Hause, 1936; Comroe and Schmidt, 1938, Gellhorn and Lambert, 1938).

Class I Cyclostomata

An exhaustive examination of the literature of this group indicates that no work has been done to determine the presence or absence of the pressoreceptors.

Since this group differs from the Elasmobranchs only in the lack of jaws and paired appendages and since Lutz (1930) pointed out physiologically the presence of pressoreceptors in the Elasmobranchs, it is possible that some primitive system exists here too.

Class II Pisces

Subclass I Elasmobranchii

Most of the work done on the Elasmobranchs has been done on the Selachians. In Squalus acanthias cardiac inhibition was obtained by increasing the pressure within the gill vessels and heart and by direct stimulation of sensory endings scattered widely throughout the body (Lutz & Wyman, 1932). In order to demonstrate cardiac inhibition resulting from pressure changes, Lutz & Wyman (1932) ligated the ventral aorta between its first and second branches and inserted a cannula in the ventral aorta anterior to the ligature. They connected the cannula with a burette filled with urea-saline solution. By opening the connection between the cannula and the burette, thus suddenly increasing the pressure within the gill vessels arising from the first branch of the aorta, cardiac inhibition was brought about. After the first sudden increase in pressure, regardless of the further increase, the initial inhibition was not increased or continued. Thus it was pointed out that the effective physiological stimulus is the initial increase of pressure and not the continual flow of fluid through the gill vessels. The afferent pathway includes the branchial nerves, and the efferent pathway includes the vagus nerve to the heart. When the fifth branchial nerve and the ramus visceralis were cut on the right side and the first right branch of the ventral aorta was clamped, thus leaving only the left gill vessels open to stimulation, cardiac inhibition

was obtained. When the first left branch of the ventral aorta was clamped, cardiac inhibition was obtained, by stimulating the right gill vessels. The reflex pathways for cardiac inhibition, consequently, are both unilateral and crossed. Lutz & Wyman, (1932) also pointed out that the heart of the Elasmobranchs is in a state of tonic inhibition maintained reflexly with each heart beat. This reflex may be homologous with the carotid sinus reflex found in mammals.

Since there are no vasomotor reflexes in the Elasmobranchs, the cardiac reflex is of utmost importance in the regulation of both the blood pressure and the heart rate (Lutz and Wyman, 1932).

This reflex is an extremely important protective mechanism. When the pressure in the gill region is increased by contraction of the branchial muscles during an ejection reflex, the walls of the afferent vessels may be very easily injured except for this mechanism (Lutz and Wyman, 1930).

No attempt has been made to determine histologically the nature and distribution of the receptors concerned with the cardio-inhibitory reflex in Elasmobranchs.

Class III Amphibia

Subclass Urodela

In the aquatic amphibian, Necturus, the region of sensitivity to changes in the blood pressure is confined to the gill region. (Lutz & Wyman, 1932). This represents a more specialized condition than is found in the fishes.

Subclass Anura

In the land amphibia the condition becomes even more specialized. A bulbous structure, the carotid gland, is located at the base of the internal carotid artery. This structure consists of two main parts, the pars cavernosa, the anterior division, in which lies the pars capillaris, and the posterior portion, the "[illegible]" zone into which the internal and external carotid arteries empty. The gland is composed of smooth muscle, loose connective tissue, and some pigment cells (Zimmerman, quoted by Gaupp (1934). A branch of the ninth nerve innervates the region (Meyer, 1927; Boyd, 1933; Smith, 1938).

An increase in pressure within the aorta brings about a decrease in the heart rate (Kuno and Brucke, 1914, quoted by Smith, 1938). This would indicate the presence of an aortic depressor nerve similar to the one present in mammals. Central stimulation of the glossopharyngeal nerve also decreased the heart rate and the blood pressure. Since the glossopharyngeal nerve sends a branch to the carotid gland (Meyer, 1929) as in the mammals, the carotid gland may be homologous with the mammalian carotid sinus.

The sensory areas in the carotid gland are derivatives of the third branchial arch and those in the aorta are derivatives of the fourth arch of the embryo (Maurer, 1888 and Marshall, 1890, quoted by Ask Upmark, 1935; Koch, 1931).

Using the Nonidez' modification of the Cajal Technique, the writer made sections of the carotid gland together with the carotid and aortic arteries of Rana pipiens. As soon as the tissue was removed from the body of the frog, it was fixed with a twenty-five per cent solution of chloral hydrate in fifty per cent alcohol for twenty-four hours. The tissue was then removed and put in a solution of sixty cubic centimeters of ninety-five per cent alcohol plus four drops of strong ammonia for twenty-four hours. After washing the tissue in distilled water for one or two minutes, it was put in a three per cent solution of silver nitrate for six or seven days in an incubator in the dark. After the alloted time the tissue was rinsed in distilled water and reduced for twenty-four hours in a three per cent solution of pyrogallic acid. Then the tissue was later washed in distilled water for one or two hours and dehydrated in the usual manner. After dehydration the block was left in amyl acetate until it was cleared.

Upon study of the slides, the writer found nerve fibers present in the carotid gland, the aortic and carotid arteries, and the wall of the auricle. The nerve fibers in the carotid gland are concentrated in the region of the pars capillaris intimately associated with the epithelial cells. Nerve fibers are also present in the media and adventitia of the aortic and carotid arteries. No nerve fibers were seen in the intima. As yet, no nerve endings have been definitely seen.

The relative position of the fibers, however, corresponds with that of the pressoreceptors in the mammal, and it seems more than likely that pressoreceptor nerve endings are present.

Class IV Reptilia

Order Squamata

In this group, Bhatia and Dayal (1933, quoted by Ask Upmark, 1935) have found a carotid 'gland" at the bifurcation of the carotid artery. This body may be similar to the carotid gland previously seen in the Amphibia.

Order Chelonia

Although no bulbous swelling is present at the base of the internal carotid artery, this portion is very richly supplied with nerves. Branches of the glossopharyngeal, vagus, hypoglossal, and sympathetic nerves supply this region (Ask Upmark, 1935).

This area may be homologous with the carotid sinus in the mammal, but conclusive proof can be obtained only through the use of physiological and histological methods.

No sensory (afferent) endings which might be concerned with cardio-vascular reflexes have been described on the aortic or subclavian arteries.

Order Crocodilia

From the right aortic arch two brachiocephalic trunks arise. The right trunk then branches into the subclavian and the external carotid; whereas the left trunk divides into the

subclavian artery, the external carotid, and the internal carotid arteries. The internal carotid artery continues along the vertebral column as the prevertebral artery, and in the region of the neck branches into two carotid arteries, the right and the left. Each of these then divides into three branches. One branch joins the external carotid, one goes to the brain, and the other goes in a more dorsal direction to the eye (Ask Upmark, 1935).

The region at the bifurcation of the brachiocephalic trunk into the internal carotid, and the point of anastomosis between the internal and external carotid arteries are richly supplied with branches from the glossopharyngeal, vagus, and sympathetic nerves (Ask-Upmark, 1935). ✓ "It is remarkable to find that the innervation of the latter point is more pronounced on the right side where the origin of the internal carotid from the common carotid has disappeared; whereas the innervation of the lower end was present only on the left side where the base of the internal carotid was preserved." (Ask Upmark,1935). ✓

A question now arises as to which one is to be considered the carotid sinus. This can be settled only by histological, physiological, and embryological work.

No mention has been made in the literature of endings on the subclavian or aortic arteries.

Class V Aves

The pressoreceptors in the chick include endings in the carotid sinus, on the antero-lateral, postero-lateral, and antero-medial surfaces of the aorta, and on the small blood vessels that supply blood to the carotid body (Nonidez, 1935). The endings in the carotid sinus are terminations of the intercarotid or sinus nerve of Hering. This nerve receives myelinated fibers from the ganglion nodosum of the vagus and non-myelinated fibers from the 'tronco prevertebrale precarotideo' (Nonidez, 1935). The fibers from the 'tronco prevertebrale precarotideo' have their origin in the glosso-pharyngeal nerve. The terminations of the nerve in the sinus appear as small rings or reticulated swellings in the outer third of the media between the muscle cells, and in the externa. The wall of the sinus does not differ in structure from the wall of the internal carotid artery except in the presence of nerve endings (Nonidez, 1935).

The aorta receives nerve fibers from the right aortic depressor nerve and the accessory depressor nerve. The aortic depressor nerve arises directly from the ganglion nodosum at its caudal portion. This nerve may also receive non-myelinated sympathetic fibers from the 'tronco prevertebrale precarotideo'. These fibers end as ring-shaped, or fairly large club-shaped, swellings in the media between the smooth muscle cells of the antero-lateral and antero-medial portion of the aorta (Nonidez, 1935). In some cases

the fibers may even reach the endothelium. The accessory depressor nerve also arises from the ganglion nodosum just above the point of origin of the aortic depressor nerve. Its fibers terminate in the media and externa on the postero-lateral surface of the aorta. This nerve may have ganglion cells along its course in the externa of the aorta. (Nonidez, 1935, and Brown, 1935.)

Nerve endings also occur on the walls of the small arteries supplying the carotid glomus. The reticulated terminations in this case are usually flattened (De Castro, 1928; Muratori, 1935).

Class VI Mammalia

In most mammals the pressoreceptors include endings in the carotid sinus, on the right subclavian artery, and on the arch of the aorta. The carotid sinus is supplied by a branch of the glossopharyngeal nerve, the sinus nerve, and a branch of the vagus. The aortic depressor nerve, which arises by two roots, one from the vagus and one from the superior laryngeal, supplies the wall of the aorta and the right subclavian (Heymans and Bouckaert, 1930).

The carotid sinus is the chief pressoreceptor organ. It is located at the base of the internal carotid or at the base of the most important artery destined for the cranial region (Ask Upmark, 1935). It is plentifully supplied with

nerve endings, and its structure will be described in detail later.

Subclass Marsupialia

Since most of the animals in this group have the peculiar characteristic of hanging by their tails or paws, one would expect to find a large carotid sinus, or other highly specialized pressoreceptor organ.

In Didelphys, the only species investigated, the base of the internal carotid has a thinner wall and is of greater size than the rest of the artery. It is supplied by branches from the glossopharyngeal, the vagus, the hypoglossal, and the sympathetic nerves.

No histological study has been made of the carotid sinus or wall of the aortic and subclavian arteries in order to determine the presence or absence of pressoreceptor nerve endings.

Subclass Monadelphia

Order Cetacea

There is a marked dilatation at the origin of the internal carotid artery. The adventitia in this particular region is much thicker than in other parts. This region receives branches from the glossopharyngeal and the vagus nerves and thus may be homologous with the carotid sinus found in the higher mammals. (Ask Upmark, 1935).

Order Ungulata

Suborder Perissodactyla

In Tapirella, the only species investigated, the internal carotid artery arises in common with the occipital artery from the common carotid. This common origin presents no dilatation, but is plentifully supplied with branches of the glossopharyngeal, vagus, and sympathetic nerves. This common origin may be homologous with the carotid sinus found in the dogs and cats.

Suborder Artiodactyla

In Camelus bactrianus the carotid bifurcation into the external, lingual, and occipital arteries is supplied with branches from the glossopharyngeal, vagus, and the sympathetic nerves. In the genus Llama the same condition persists, except that there is a slight dilatation at the base of the internal carotid. In the genus Capra the internal carotid artery has a common origin with the occipital artery. This region is also supplied with branches from the glossopharyngeal, vagus, and sympathetic nerves. (Ask Upmark, 1935).

Order Rodentia

Suborder Hystricomorpha

In the guinea pig the pressoreceptors include endings in the carotid sinus, on the right subclavian artery, on the arch of the aorta, and on the innominate artery. The carotid sinus is supplied mainly by a branch of the sinus

nerve of Hering. The aortic depressor sends fibers to the externa and outer third of the media of the aorta, the subclavian, and the innominate arteries. The aortic nerves carry a relatively small number of thick afferent fibers (Nonidez, 1935).

Suborder Myomorpha

The pressoreceptors of the rat are identical with those present in the guinea pig. The right aortic depressor is relatively thin and supplies the base of the right subclavian (Nonidez, 1935). On the left side the left aortic depressor nerve sends fibers to the arch of the aorta, the subclavian, and the innominate arteries.

Suborder Lagomorpha

The pressoreceptors in the rabbit include the endings in the carotid sinus, on the subclavian, innominate, and aortic arteries. The right aortic depressor nerve, an independent nerve trunk on the right side of the neck mesial to the cervical sympathetic or between it and the vagus, sends fibers chiefly to the super-lateral portion of the right subclavian, and the left aortic depressor nerve, an independent nerve on the left side of the neck, sends fibers to the arch of the aorta (Heymans and Bouckaert, 1936; Nonidez, 1935). This nerve may also send fibers to the small fibrous blood vessels supplying the aortic glomus and to the innominate artery. The intercarotid, or sinus nerve of Hering,

sends fibers to the adventitia of the carotid sinus.

The terminations of these nerves are found in the externa and in the outer third of the media of the vessel concerned. The fibers never reach the intima as they do in birds. No ganglion cells were ever seen in the wall of the aorta or subclavian artery. (Nonidez, 1935).

The carotid sinus nerve arises from the glossopharyngeal nerve; whereas the aortic depressor nerve arises by three roots, the vagus, the superior laryngeal, and the cervical sympathetic (Nonidez, 1935). The left aortic depressor nerve is larger than the right because of its wide field of distribution. Both the right and left aortic nerves furnish pressoreceptors to the branches of the arteries supplying the aortic glomera. (Nonidez, 1935). A few of the fibers from the anterior branch of the left aortic nerve and from the aortic branch of the vagus may terminate as pressoreceptors in the ductus arteriosus. (Nonidez, 1935).

The terminations of these various nerves all possess ring-like, or club-shaped, reticulated swellings in which the neurofibrils are plainly visible. The endings on the ductus arteriosus, however, are much simpler than those in the aorta. The reticulated swellings may be either terminal or subterminal. This difference in size and position of the terminations may account for the different degrees of responses upon stimulation. "Since the excitant in

this case is entirely mechanical, the passive approximation of the connective tissue fibers during stretching of the wall will first compress the thicker reticulated swellings of the nerve ending initiating periodic discharges. A higher arterial pressure will presumably intensify the compression and affect the thinner portions of the arborizations." (Bronk and Stella, 1932). The coarse arborizations have a lower threshold than the thinner more diffuse arborization.

Order Insectivora

In *Erinaceus europoeus*, the only specimen studied, a slight bulb-like dilatation is present at the base of the internal carotid artery. The internal and the occipital arteries emerge together from the dilatation. It is supplied with branches from the glossopharyngeal, vagus and sympathetic nerves. It is a question, however, whether this is the carotid sinus.

Order Chiroptera

In the Australian bat, an animal that continually hangs from its claws with head down, one would expect to find a very large and well-developed carotid sinus. The internal carotid, however, possesses no bulbous dilatation at its origin, but is very richly supplied with branches of the glossopharyngeal, vagus, and hypoglossal nerves.

Order Carnivora

Suborder Fissipedia

In the dog the pressoreceptors include endings in the carotid sinus, on the external carotid, occipital, right subclavian, innominate, pulmonary, left subclavian, and aortic arteries.

The carotid sinus is a bulb-like dilatation on the base of the internal carotid. Its walls are thinner, less muscular, and more elastic than the carotid artery (Ask-Upmark, 1935). Nerve endings with bulbous swellings in which the neurofibrils are plainly visible, are present in the adventitia between the collagenous fibers, and in the outer third of the media. These nerve endings are terminations of a branch of the glossopharyngeal nerve, of the superior cervical ganglion of the sympathetic, and of the vagus.

The remaining terminations occur in the externa or outer third of the media in the particular vessel involved. These terminations are the endings of the aortic depressor nerve, which arises by two roots, one from the vagus, and the other from the superior laryngeal nerve. This nerve is not an independent nerve in the dog, but courses along as a separate bundle in the vago-sympathetic trunk. Upon leaving the vago-sympathetic trunk at the level of the inferior cervical ganglion, the fibers of the aortic depressor nerve do not go directly to their respective arteries as in the rabbit,

cat, and guinea pig, but join other nerves. The right aortic depressor nerve after leaving the vago-sympathetic trunk enters the right cardiac nerve. It then continues to the aortic nerve and finally reaches its termination in the distal portion of the innominate artery and base of the subclavian (Nonidez, 1937). The major part of the fibers are the sympathetic postganglionics from the inferior cervical ganglion. The nerve terminations are similar to those found in the cat. "Upon reaching the level of the inferior cervical ganglion the fibers of the left aortic bundle join an anastomosis between this ganglion and the left cardiac nerve except for a number of them which enter the ganglion to course with a bundle of post-ganglionics running as a thin nerve between the innominate artery and the left subclavian. The aortic fibers within the left cardiac nerve reach the externa of the aorta and end in pressoreceptor arborizations in the externa and outer third of the media. The nerve, however, does not end in this vessel, for some of the aortic fibers run on the anterior surface of the ductus arteriosus and are distributed over the anterior aspect of the bifurcation of the pulmonary trunk, forming a second pressoreceptor area not present in the rabbit and cat, although in these animals there are pressoreceptor endings in the wall of the ductus arteriosus." (Nonidez, 1937). The sympathetic nerve carrying aortic fibers on the left side is not as large as the cardiac

nerve. It sends branches to the innominate and to the left subclavian arteries. When it reaches the aorta it contributes to the formation of the arch of the aorta.

The largest number of nerve terminations occurs in the anterior surface of the aorta instead of in the dorso-posterior region as in the case of the rabbit. No pressoreceptor endings are present in either the abdominal or the descending portion of the aorta. This is also true of the guinea pig, rabbit, and cat.

Stimulation of any of the pressoreceptors by an increase in blood pressure will reflexly bring about a drop in blood pressure, retardation of heart rate and respiration. The afferent pathways include the carotid sinus nerve and the aortic depressor nerve. The efferent pathways include motor neurones, autonomic and cerebro-spinal which innervate the heart, blood vessels and respiratory muscles. The afferent nerves maintain a state of tonic inhibition over the centers in the medulla, since when they are cut, there is an increase in the heart rate, respiration, and blood pressure (Comroe and Schmidt, 1940).

These different effects seem to be independent of one another. There may be a reflex respiratory effect without any circulatory effect whatever. Whether different types of nerve terminations are involved is still an unsolved problem. "The respiratory mechanism appears to be more sensitive to

changes in pulsation than to changes in mean pressure." (Schmitt, 1940). The endings in the aortic arch are more important in the regulation of heart rate than are those in the carotid sinus (Schneyer, 193[illegible]). A cardiac reflex set up in the carotid sinus may be entirely reversed by stimulation of the aortic arches. The cardiac reflex responds sooner and is more poorly maintained than the respiratory effect (Winder, 1937).

These nerve endings thus far discussed are thought to be depressor endings, since on stimulation with increase in pressure they cause cardiac inhibition, a decrease in the blood pressure, and a decrease in the rate of respiration. It has also been shown that decreasing the blood pressure does not arouse a pressor activity, since after denervation there is no further fall in the blood pressure (Hering, 1927, quoted by Sweeny, 1940). Wright (1933, quoted by Sweeny, 1940) still claims, however, that there are pressor endings present which are stimulated by either a fall in pressure or an increase in pressure at very low pressure levels and bring about an effect opposite to that brought about by stimulation of the depressor endings. In support of this statement he showed that on raising the pressure in the carotid sinus of the cat from zero to fifty millimeters, he obtained a reflex rise in pressure. Heymans and Bouckaert (1933, quoted by Sweeny, 1940) had previously obtained a similar response in the dog. McDowall (1933, quoted by Sweeny, 1940) showed

that after a hemorrhage, section of the vagus may further decrease the blood pressure and stimulation of the central end of the cut vagus nerve may increase the blood pressure. This is in agreement with Wright's view on the presence of pressor fibers. [illegible] (19[illegible]), however, using the same technique as McDowall obtained results contrary to those of Wright. Sufficient experimentation has not been carried out to warrant any conclusion regarding the presence or absence of pressor fibers.

The anatomical arrangement of these endings presents an advantageous position for stimulation by changes in pressure. Stimulation is brought about by a distension of the wall and the response is directly proportional to the amount of distension ([illegible] and [illegible], [illegible]).

The pressoreceptors of the cat present the same arterial localization and nervous supply for the most part as the dog. The carotid sinus of the cat, however, is supplied by a branch of the hypoglossal nerve in addition to the other nerves present in the dog. In the cat the aortic depressor nerve is an independent nerve and some of the fibers are quite large. Most of the terminal arborizations of the aortic fibers lie in the adventitia of the arteries or between the latter and the media. There are also some endings present in the media. In such instances the branches of the arborizations are situated between the elastic membranes.

In no case do they reach the lumen as in birds. The enlargements may be terminal, subterminal, or may be placed somewhere in the course of the [illegible]. In the case of the arborizations located in the outer portion of the media, the reticulated enlargements lie between the fenestrated elastic membranes of this layer ([illegible], [illegible]).

Order Primates

Suborder Lemuroidea

In *Propithecus* [illegible], the only specimen examined, there is a balloon-like dilatation at the base of the internal carotid artery. It is supplied by branches of the glossopharyngeal, vagus, and the sympathetic nerves. ([illegible], 1935).

Suborder Anthropoidea

In monkeys, chimpanzees, and man a balloon-like dilatation is present at the base of the internal carotid artery ([illegible], [illegible]; Boyd, 1937). It is referred to as the carotid sinus and is supplied by the vagus, glossopharyngeal, and hypoglossal nerves. Anastomoses are often present between the vagus and the glossopharyngeal nerves in the carotid sinus. This is not true of any of the vertebrates thus far studied (Cordier and Coulouma, [illegible]). In man the branch of the glossopharyngeal or sinus nerve is a single "strand or a bunch of fibers, lying usually in the posterior part of the space between the internal and

external carotid and running downward toward the sinus over the wall of which it ramified." (Ian Hill, 1933).

Nerve endings are also present on the walls of the aorta and right subclavian arteries. These endings are terminations of the aortic depressor nerve. These pressoreceptor endings are similar in histological structure to those already described in the dog.

Stimulation of any of these pressoreceptors brings about the same responses as in the dog. The reflexes brought about by stimulation of any of the pressoreceptor endings are bilateral rather than unilateral as in the cat and dog. In man each vagus nerve innervates the sino-atrial node (Hoff and Nahum, 1935). In the dog, however, only the right vagus innervates the sino-atrial node. "The fibers of the lowest threshold in the vagus innervate the S. A. node." (Hoff and Nahum, 1935).

In man as well as in the dog the nerves maintain a state of tonic inhibition (Mihaescu, Jacobovici, and Pop, 1929). The function of the pressoreceptors is the same here as in the case of the dogs (Enderle, 1924, quoted by Ian Hill, 1933). Enderle and Tillman (1924, quoted by Ian Hill, 1933) showed that increase in pressure within the carotid sinus caused reflexly a decrease in blood pressure from one hundred five to sixty-seven millimeters of mercury. They also obtained a reduction in heart rate from eighty to seventy-two beats per minute.

Part II Chemoreceptors

Since the physiology of the carotid sinus was known long before the function of the carotid body was known, it had been believed that the carotid sinus region played a dual function, that of a chemo- and a pressoreceptor. However, it was soon shown that by tying off the carotid sinus below the emergence of the recurrent laryngeal nerve, the pressoreceptor activity was abolished without any effect on the chemoreceptor activity (Bouckaert, Dautrebande, and Heymans, 1930). The actual localization of the chemoreceptors was done by Schmidt (1937). In the dog, he ligated the occipital artery at its origin and reduced or abolished the reflex effects of alterations in the gas content of the blood in the carotids. Gollwitzer and Meier (1934, quoted by Comroe and Schmidt, 1940) obtained the same results by injections of alpha-lobeline and sodium cyanide. Neither could decide whether the chemoreceptors were located in the carotid body or in the first portion of the occipital artery. Comroe and Schmidt (1940) showed that the effects of intra-carotid injection of small doses of lobeline or cyanide were entirely abolished on clamping the small artery to the carotid body and restored on opening this vessel. This seemed to show that the carotid is the only location of importance for chemoreceptors in this region. They also concluded, from vessel anastomoses and perfusion experi-

ments, that the pressoreceptors are limited to the carotid sinus region, and are not present in the occipital artery or carotid body.

The histological structure of the organs containing the chemoreceptor endings is practically similar in the different forms of vertebrates studied. The organs are very richly supplied with blood vessels. There is a special arteriole and venule to each group of cells. Sinusoids or thin-walled capillaries are very abundant. Around the arteries is a net work of nerve fibers derived from the glossopharyngeal, vagus, hypoglossus, and the cervical sympathetic. The aortic depressor is one of the more important nerves. Each cell of the carotid body has a well-marked Golgi apparatus placed between the nucleus and the side of the cell in contact with the blood vessel. The carotid body is the largest of the paraganglia, and like the other epithelial bodies, it is composed of cords of polygonal cells near the endothelium of the blood vessels. Ganglion cells along the cords of the glomera are very scarce and unusual. Brown (1955) suggested that they represented dislocated ganglia from the ganglion nodosum of the vagus.

The chemoreceptors are more widely scattered than are the pressoreceptors. They include the carotid and aortic bodies, the paraganglion supracardiale, the paraganglion supracardiale superius, the paraganglion supracardiale

inferius. All these are not present in any one form and their presence in the various forms of vertebrates investigated will be discussed. The carotid body is a derivative of the mesoderm of the third branchial arch and the ectoderm of the glossopharyngeal nerve (Boyd, 1937). The aortic body arises from the fourth arch and the ectoderm of the vagus nerve; and the paraganglion supracardiale, the paraganglion supracardiale superius and the paraganglion supracardiale inferius from the sixth arch (Nonidez, 1935). The embryology will be discussed in detail in the animals in which it has been worked out.

These bodies are stimulated by changes in the respiratory gases of the blood, or by changes in the metabolism within the tissue itself. As previously stated in the introduction, earlier investigators considered the centers in the medulla of prime importance in response to oxygen lack. Gesell (1933) claimed that oxygen lack increased the acid metabolism of the respiratory center. Bouckaert, Dautrebande, and Heymans (1930) were the first to suggest that the carotid body region is affected by oxygen lack, carbon dioxide increase, or injection of alpha-lobeline and sodium cyanide. Since this important contribution, a controversy has arisen as to whether oxygen lack or carbon dioxide increase has the greater effect on the carotid body region.

Gesell, Lapides, and Levin (1940) have shown that the respiratory tracing during carbon dioxide administration remains the same after complete denervation of the chemoreceptive areas; whereas the tracing during oxygen deficiency is considerably altered after chemoreceptive denervation. This indicates that the chemoreceptors are more sensitive to a lack in oxygen and the respiratory center is more sensitive to carbon dioxide increase. Others claim, however, that the chemoreceptors are more sensitive to both oxygen and carbon dioxide changes than is the respiratory center (Heymans, 1939, quoted by Gesell, Lapides and Levin, 1940). Still others claim that the chemoreceptors are accessory organs used in time of emergency, and that during normal breathing the centers in the medulla are of greatest importance (Comroe and Schmidt, 1938; Schmidt, Dumke, and Dripps, 1939; Schmidt and Comroe, 1940). Others suggest that the chemoreceptors and the centers participate jointly in the control of normal breathing, and a higher degree of intensity of chemical stimulus is needed to affect the center when the chemoreceptors are denervated (Bernthal and Weeks, 1939). Comroe and Schmidt (1938) pointed out that the carotid body receptors are more resistant than the cells of the center to depression by narcotics, anoxia, and to excessive carbon dioxide tension. This reflex mechanism keeps respiration going when the cells of the center have

lost practically all of their ability to respond to changes in their immediate environment. During anesthesia the response of the centers in the medulla to oxygen lack is either missing or reduced (Heymans and Bouckaert, 1939; Schmidt and Comroe, 1940.) This may account for the difference in opinion as to the relative importance of the centers in the medulla and the chemoreceptors, in their response to carbon-dioxide increase and oxygen lack.

As pointed out earlier, alpha-lobeline and sodium cyanide have the same effect as oxygen lack on the chemoreceptors. Cyanide and lobeline act by preventing the formation of the enzyme oxidase, which is necessary for oxidation to take place. Without oxidase there is an accumulation of acid and this acid may act as a stimulus. This would seem to indicate that the activity of the chemoreceptors depends not only upon changes in the respiratory gases in the blood, but also upon changes in its own metabolism. The formation of lactic acid is necessary for its excitation (Winder, 1937; Bernthal, 1939). Local increase in temperature causes an increase in the metabolism of that particular region, and if the environment remains the same the degree of excitation consequently increases (Bernthal and Weeks, 1939; Winder, 1937). Use of iodoacetic acid prevents the response of the chemoreceptor to anoxia (Winder, 1937).

The degree of excitation of the chemoreceptors is directly proportional to their internal acidity (Bernthal, 1938).

The aortic bodies, supracardiale paraganglion and others all play minor roles as chemoreceptive organs. The carotid body is the most important.

Class I   Cyclostomata

In Cyclostomata, no investigation, as far as I have been able to ascertain, has been made on the presence or absence of these chemoreceptors.

Class II   Pisces

Subclass   Elasmobranchii

The Elasmobranchs, sting ray and sand sharks, have a very large carotid gland. It is twenty times larger than the one found in man. "It lies in the posterior cardinal sinus and is attached to its posterior wall by only a few strands of fibrous tissue, a few nerve fibers and the axillary artery which runs through its upper pole." (Christie, 1933). The nerve fibers arise in the vagus nerve and from the gastric ganglion. This structure had been described earlier by Lutz as the suprarenal gland (1927).

An exhaustive survey of the literature disclosed no reference to this body as the carotid gland by anyone other than Christie. Since Christie does not mention Lutz's work in his bibliography or text, it may be concluded that Lutz's assumption is correct. In addition, it does not

seem at all plausible that a carotid gland would be so large in the Elasmobranchs as described by Christie.

Class III Amphibia

Subclass Urodela

I was not able to find any literature regarding the aquatic amphibia.

Subclass Anura

Oxygen lack in the frogs causes an increased rate of respiration. When the carotid gland is denervated oxygen lack has no effect. This would seem to indicate that the carotid gland does contain chemoreceptors (Smith, 1939). The aortic region also responds to changes in the respiratory gases in the blood, but the carotid region is more important. The carotid gland does not react to changes in the carbon dioxide content of the blood since the carotid arteries do not carry blood containing carbon dioxide. Carbon dioxide is eliminated mainly through the skin (Smith, 1939). As in the mammals the carotid gland is derived from the third branchial arch. No histological studies have as yet been made to determine the presence or absence of the particular type of nerve ending involved in chemoreceptive activity, although the writer has found nerve fibers which may be chemoreceptors.

Class IV Reptilia

No work has been done as far as I have been able to ascertain to determine the presence or absence of the chemoreceptors.

Class V. Aves

The carotid body and paraganglion supracardiale aorticum contain the chemoreceptors in the chicks (Nonidez, 1935).

The carotid body is located at the bifurcation of the common carotid into the internal and external carotid arteries. A small artery that arises from the bifurcation constitutes its main blood supply. It is innervated by a branch of the carotid depressor nerve, which arises from the ganglion nodosum of the vagus, and by a branch of the 'tronco prevertebrale precarotideo', which consists of non-myelinated sympathetic fibers arising from the glosso-pharyngal nerve (Terni, 1931, quoted by Nonidez, 1935). Since it arises from the glossopharyngeal nerve it may be considered homologous with the sinus nerve of Hering found in the mammals. The carotid body consists of large epithelial cells richly supplied with blood vessels and nerves.

The paraganglion supracardiale aorticum consists of large encapsulated nerve endings in the media above the opening of the aorta. The encapsulated endings consist of an outer thin layer of connective tissue. Inside this layer there is a large number of round cells with round or oval nuclei. The cytoplasm of these cells is clear or slightly granular (Nonidez, 1935). Each contains a well defined Golgi apparatus. These cells are identical with those found in the carotid body. The encapsulated nerve endings are separated from each other by spaces in which course the nerve fibers destined for

the corpuscle. The nerve fibers enter the capsule at any point. The endings of these fibers possess either the bulbous swellings or delicate rings encircling the cells. Some of these endings are in direct contact with the cell, others are in the intercellular spaces. The nerve endings are terminations of a branch of the aortic depressor nerve. The aortic depressor may be fused with the accessory depressor or with the nerves supplying the glomus aorticum.. Only the right aortic depressor nerve is present. On the left side the subclavian artery still persists.

Whether this structure is really homologous with the paraganglion aorticum or the aortic body in the mammals is still a question to be decided. It could be determined embryologically, if in no other way. In mammals, the aortic body is a derivative of the fourth aortic arch, while the paraganglion supracardiale is a derivative of the sixth aortic arch (Nonidez, 1935).

Class VI Mammalia

Subclass Monodelphia

Order Ungulata

Suborder Artiodactyla

The carotid body is the only chemoreceptor that has been described in the calf. The carotid body is first seen as a thickening of mesoderm in close relation

to the third aortic arch on its ventral and external side. In the fifteen millimeter stage it receives a branch from the glossopharyngeal nerve (Smith, 1924, 1925). The ganglion nodosum and the superior cervical sympathetic ganglion come into the region of the carotid body. The vagus and the pharyngeal branch of the ninth nerve anastomose at the twenty-five millimeter stage. Sympathetic ganglia are grouped peripherally and develop into large lobulated masses (Smith, 1935). As the embryo grows, the tissue accompanying the rich nerve supply is the one which develops faster and forms a lobulated thick outer stratum.

The carotid body receives its blood supply in the nineteenth millimeter stage from a branch of the external carotid artery. Later it receives its blood supply from a branch of the internal carotid artery. The arteries do not terminate in the carotid body but pass beyond it and terminate in the surrounding tissue. The capillaries of the carotid body possess a definite wall and do not form a glomerular arrangement. The smaller vessels on the arterial side are thicker than those on the venous side. Muscle cells are present only on the large entering blood vessels. Embryonic cellular elements of sympathetic origin are derived from cells originating from both the cervical and cranial sympathetic.

Chromaffin cells are very abundant. They are larger, have a more lightly stained nucleus than the non-chromaffin cells. The chromaffin cells are similar to the cells of the medulla of the suprarenal and, like them, are associated with the sympathetic system in their development.

From the description of the embryology one can conclude that the carotid body is intimately associated with the vascular network of the third arch.

Order Rodentia

Suborder Hystricomorpha

In the guinea pigs the only chemoreceptors present are the carotid body and the paraganglion supracardiale aorticum. The carotid body is located in the angle formed by the bifurcation of the common carotid into the internal and external carotid arteries. Rabl (1932, quoted by Boyd, 1937) pointed out the derivation of the carotid body from a differentiation of the mesodermal cells related to the internal carotid artery. The glossopharyngeal nerve is very closely allied to the carotid body.

The aortic nerves carry a relatively small number of thick afferent fibers. The distribution of the aortic nerves is very similar to that in the rabbit and cat. The aortic glomera are usually infra-aortic. The right glomus occurs below the subclavian of its sides; while the left is usually located below the arch of the aorta. The aortic body is a

dense structure composed of groups of cells separated from each other by strands of connective tissue, containing the smaller vessels. It soon becomes infiltrated with fat cells and is more densely fibrous. It lacks chromaffin cells. "In the glomus of the guinea pig there appear a large number of nerve branches with peculiar terminations. In some cases they look as rather simple, bifurcated reticular swellings which may embrace a glomus cell or one or more smaller cells of a fibroblastic nature, belonging to the thin connective tissue capsule of the cord or to the externa of the smaller arterial branches. In other instances these terminations are more complex and may give rise to a basket enclosing one or more epithelial cells. This latter arrangement is a very characteristic feature of the paraganglion aorticum of the cat.' (Benitez, 1955).

Suborder Myomorpha

In the rat the carotid body is the only chemoreceptor found discussed in the literature. The carotid body develops in much the same way as in the calf. A small group of sympathetic fibers from the carotid body may be traced to the hypoglossal nerve in the seventeen-day embryo. No such connection exists in the calf. The sympathetic cells are peripheral but not as profuse as in the calf (Smith, 1924, 1926). The carotid body receives

its main blood supply at first from the external carotid or occipital arteries, and its nerve supply from a branch of the glossopharyngeal nerve. No chromaffin cells are present.

Suborder Lagomorpha

In the rabbit the chemoreceptors are included in the carotid body, the aortic bodies, and the paraganglion aorticum. The aortic depressor nerve and the sinus nerve of Hering are the two afferent nerves. The left aortic depressor nerve arises by two roots, the vagus and the superior laryngeal. It sends fibers to the aortic body above the arch of the aorta, and to the supracardiale paraganglion aorticum. The right aortic depressor nerve supplies the aortic body (Nonidez, 1936). The sinus nerve of Hering supplies the carotid sinus.

The endings are more diffuse than they are in the rat. The right aortic glomus occurs in the angle formed by the subclavian and the common carotid; whereas the left aortic glomus lies above the aorta medial to the left subclavian. The right aortic glomus receives blood through branches of a small artery arising directly from the arch of the aorta or from the left subclavian. The arteries, however, do not terminate in the glomus but continue to the surrounding tissue.

Although the aortic glomus artery does not differ in structure from other arteries, its proximal portion and the large branches within the glomus have a thick adventitia, in which are found round nuclei. It appears more like a vein than an artery. The arterial branches supplying the glomus have pressoreceptor endings rather than chemoreceptor endings. These pressoreceptor endings, however, are restricted to the blood vessels that terminate in the glomus, itself. The branches which pass beyond the glomus to supply the surrounding tissue do not have pressoreceptors and their externa is not thick nor cellular.

"After dividing among the group or cords of epithelioid cells of the glomus the arterial branches are continued into the arterioles and capillaries. One or more pre-capillary arterioles cross the thin connective tissue capsule enveloping each epithelial cell group breaking into thin-walled capillaries among the glomus cells. The walls of the capillaries are exceedingly thin and contain few nuclei. Since there is barely any connective tissue between the wall of each capillary and the glomus cell, most of the latter seem to be in direct contact with the endothelium, a condition also observed in the carotid body." (De Castro, 1926; Nonidez, 1935).

Order Carnivora

Suborder Fissipedia

In the dog the chemoreceptors include the carotid body, the paraganglion supracardiale superius, and the paraganglion supracardiale inferius.

The carotid body is found on the occipital artery which arises from the carotid sinus proper. Denervating the carotid sinus, however, has no effect on the chemical activity of the carotid body (Heymans and Bouckaert, 1950).

The carotid body consists of large epithelial cells of a non-chromaffin nature. These cells are abundantly supplied with nerves from the glossopharyngeal nerve. The external carotid and occipital arteries make up the vascular supply of this organ. As the external carotid artery approaches the carotid body the walls become thinner, the muscle begins to disappear, but the elastic tissue is increased. This is much the same structure as is found in the carotid sinus. The beginning of the occipital artery is somewhat dilated and its wall is composed chiefly of elastic tissue. It is called the occipital sinus due to its similarity with the carotid sinus. From the occipital arises a branch also elastic in nature at its beginning, and from this branch originates the artery which supplies the carotid body (Addison, 1940).

The paraganglion supracardiale superius and the paraganglion supracardiale inferius are both located beneath the arch of the aorta.

Localization of the aortic chemoreceptors in the aortic body rests upon the anatomical similarities between this and the carotid body and upon the physiological experiments of Comroe(1939). The latter was able, by intra-aortic injections of cyanide or lobeline through a small catheter, which could readily be moved in and out, to demonstrate that the chemosensitive zone lies in dogs at a point at which a small artery leaves the aorta to enter the aortic body. In one experiment, he was able, by crushing the nerves in the vicinity of the aortic body, to abolish chemoreceptor activity in the aorta while retaining at least some presso-receptor function.

These bodies receive their nerve supply from the left aortic depressor. The dog lacks an independent aortic depressor nerve. The aortic depressor nerve is closely allied with the vagus sympathetic trunk, and arises by two roots, one from the vagus and one from the superior laryngeal nerves. The aortic fibers leave the vago-sympathetic trunk as it reaches the inferior cervical ganglion. Here it joins the cardiac nerve from the vagus. The left depressor nerve is a larger nerve than the right, since the left supplies the pressoreceptors in the aorta, the aortic body,

the paraganglion supracardiale superius and the paraganglion supracardiale inferius. The right supplies the subclavian artery and the aortic body. They receive their blood supply from the transverse aorta.

These receptors are sensitive both to oxygen lack and carbon dioxide excess. Oxygen lack, however, is mainly reflex and carbon dioxide increase is mainly central in its activity (Comroe and Schmidt, 1937; Gesell, Lapides and Levin, 1940).

The carotid chemoreceptors play a major role in the regulation of respiration and the aortic chemoreceptors play a major role in the regulation of blood pressure (Comroe, 1939).

In the dog Kaufman (1938) pointed out that stimulation of the carotid body inhibits the reflex contraction of the _tibialis_ _anticus_ muscle of the leg. Inhibition of the _tibialis_ _anticus_ muscle begins simultaneously with chemical stimulation of the carotid body and lasts throughout the stimulation. This would favor respiratory adjustments in time of need; indicating that the carotid body and the other chemo- and pressoreceptors are chiefly protective in nature.

In the cat the chemoreceptors include the carotid body, the aortic body, and the paraganglion supracardiale aorticum.

The carotid body in the cat is a small oval reddish body possessing chromaffin cells (Gerard and Billingsley, 1923; Smith 1924).

In 1904 it was described as an epitheliod body enclosed in a fibrous capsule. A band of fibrous tissue penetrates the body separating it into halves. From this main partition other fibers diverge dividing the body into lobules. The fibrous tissue is richly supplied with blood vessels. The lobules are composed of irregularly arranged cells separated by a delicate reticulum. The cells are large and bear an intimate relation to the blood fibers (Funke, 1904). At that time no mention had been made of chemoreceptor nerve endings. Since then, however, various chemoreceptor nerve endings have been described (Konidez, 1935). The arterial portion has sympathetically innervated smooth muscle in its walls, while the venous portion has chromaffin paraganglionic cells surrounded by sensory endings.

The paraganglion supracardiale aorticum is located below the arch of the aorta. It consists of irregular masses of roundish epithelioid cells extending from the arch of the aorta to the base of the heart, in the space between the ascending aorta and the pulmonary artery. It consists of at least two types of cells, namely large, spherical elements

containing fine yellowish granules in the cytoplasm and smaller, more irregular cells without conspicuous granulations.

The paraganglion cells are arranged into roundish groups containing variable numbers of cells. Each group of lobule is surrounded by a thin capsule which is not clearly separated from the adjacent interlobular stroma. The lobules are aggregated into larger masses of various sizes. In the newborn kitten this paraganglion receives its blood supply from the pulmonary artery (Boyd, 1937, Monidez, 1935). In the adult the blood supply has either an aortic or coronary origin (Goormatigh and Pannier, 1939). The original pulmonary blood supply of the paraganglion supracardiale aorticum becomes connected with new vessels arising from one or both coronary arteries or from the aorta itself (Goormatigh and Pannier, 1939). The vessel from the pulmonary increases its rate of cell division. This raises the endothelial lining. The endothelial walls then meet, fuse, and disappear, leaving the middle of the vessel filled with connective tissue. (Hollinshead, 1940).

The aortic glomera are small paired epithelial masses. The right aortic glomus is located above the subclavian artery near the angle formed by it and the carotid artery. The left aortic glomus, however, is situated above the aortic arch. Their histological structure is similar to

the structure of the carotid body previously described.

In the cat scattered yellowish cells exist in both the aortic glomus and the paraganglion supracardiale aorticum.

The relative parts played by the carotid and aortic chemoreceptors are much more variable in the cat than in the dog (Comroe, 1934). Usually the carotid bodies play a major role in the regulation of blood pressure, and the aortic chemoreceptors play a major role in the regulation of respiration.

Order Primata

Suborder Anthropoidea

The chemoreceptor system in man is similar to that of the dogs. The chemoreceptor endings are located in the carotid body, the paraganglion supracardiale superius and the paraganglion supracardiale inferius (Boyd, 1937).

The carotid body is derived from the third branchial arch artery and appears first as a mesodermal condensation (Boyd, 1937).

This condensation lies in the bifurcation of the common carotid artery or on the medial side of the upper end of the common carotid, in close proximity to the superior cervical ganglion. Very early in its development it receives a branch of the glossopharyngeal nerve. In the twenty millimeter stage, the cells of the condensation become

differentiated from those that make up the wall of the internal carotid. The cells of the condensation are oval or round. In the thirty millimeter stage, the cells of the condensation become separated from the cells that go to form the media and adventitia of the internal carotid artery.

The paraganglion supracardiale superius is located between the pulmonary artery and left coronary artery. According to Bussachi and Palme (1934, quoted by Boyd, 1937) it contains true chromaffin tissue. The paraganglion supracardiale inferius is located between the descending portion of the arch of the aorta and the ductus arteriosus. It also contains chromaffin tissue. In man the aortic bodies migrate from their original position above the arch of the aorta to the region below the ductus arteriosus. Here they fuse with the paraganglion supracardiale superius and as a consequence change its character. The same migration may have taken place in the dogs (Palme, 1934; Muratori, 1934).

Part III Other Epithelioid Bodies

Other groups of tissue morphologically similar to the carotid and aortic bodies such as the coccygeal body have not been investigated from the standpoint of either chemoreceptor or pressoreceptor function. Wiesel (1902, quoted by Moniez, 1935) described a collection of chromaffin

tissue situated near the origin of the coronary artery. This may be the paraganglion supracardiale aorticum. Trinci (1907, quoted by Nonidez, 1935) described chromaffin tissue related to the base of the heart. The coccygeal body, Luschka's gland, occurs near the tip of the coccyx. It receives its vascular supply from the middle sacral artery. It consists of a network of arteries surrounded by polyhedral granular cells. A sheath of connective tissue fibers binds the organ. Numerous non-medullated nerve fibers are also present.

The true nature of the function of this body is still unknown. It may, however, function as a chemoreceptor organ, since in some cases a distinct response to changes in the respiratory gases still persist after denervation of the carotid and aortic regions. (Comroe and Schmidt, 1935).

It has been shown by Heymans and his coworkers (1937) that even in the spinal dog, vasomotor reactions in both the spleen and leg may develop to changes in pressure in the aorta, though both the carotid sinus and aortic arch reflexes are excluded. The reactions depend mostly, but not entirely, on pressure changes in the areas supplied by the coelias axis and superior mesenteric arteries. The coccygeal body in that case may be the organ involved and may possess pressoreceptor endings.

Part IV Possible Glandular Function

De Castro (1926) has pointed out the cytological structure of an endocrine organ. He drew this conclusion from the following evidence: "D'offrier un cytoplasma vacuole, dont les vacuoles se trouvent a diverse degres, d'evolution, jusqu'a constituer de grandes vacuoles qui vont occuper la partie peripherique du corpuscle. Les modifications remarquees dans le noyeau quant a sa grosseur et a sa chromaticite, coincidente avec l'elaboration de vacuoles, les variations du chondriome et des granulations lipoides. L'existence de granulations lipoides et de grains impregnables par l'ormium, variable en quantite de quelques elements a d'autres. L'orientation vers le pole vasculaire du reticule do Golgi, dosage peut-etre de plus grand metabolisme du cytoplosme." Christie (1933).

Christie (1933) isolated a substance antagonistic to adrenalin from a tumor of the carotid gland in man and from the carotid gland in certain Elasmobranchs. In obtaining the extract from the tumors of the carotid gland in man, Christie (1933) thoroughly ground the gland in pure quartz sand. He then extracted the substance in the cold, using sixty-five per cent alcohol acidified with acetic acid and filtered. The alcohol was then evaporated off the filtrate at a low temperature and pressure and the residue was diluted

with water. The extract was neutralized immediately before used. He called this extract carotidin. The extract caused powerful rhythmic contractions of the virgin guinea pig uterus. These contractions differed from those that can be produced by histamine or pituitrin. Injected intravenously it resulted in a fall of blood pressure. It differs from acetyl choline in that its action cannot be abolished by small quantities of atropine.

From the carotid gland in the Elasmobranchs, sharks and sting rays, Christie (1933) obtained two different types of secretions. One is similar to adrenalin; while the other is antagonistic to adrenalin and similar to the one found in the carotid gland tumor of man. Injection of the extract into the virgin guinea pig uterus brought about the same result as the extract from the human carotid gland. Control extracts of shark muscle and spleen even in ten times the concentration of the carotid gland extracts caused no such contractions. The carotid gland extract of the Elasmobranchs produces a relaxation of the rhythmically contracting rabbit duodenum. This is similar to the effect of adrenalin. This extract also produces a rise in blood pressure which could not be produced by extracts of the muscle and spleen with even ten times the dose of the carotid gland extract.

An exhaustive study of the literature indicates no confirmation of Christie's work. Lutz, moreover, pointed out earlier that this so-called carotid gland in the Elasmobranchs is nothing more than suprarenal tissue (1927). Christie's work, therefore, must be discounted until further evidence is found by other investigators to support his statement.

Fisher (1922, quoted by Christie, 1933) has found in the calf after removal of the carotid gland listlessness and calcification of the bone may result. Klug (1884, quoted by Christie, 1933) obtained no such results. Frugoni (1913, quoted by Christie, 1933) observed with one to two kilograms of calf carotid gland extract; a slight rise in blood pressure followed by a fall. He realized that these were typical of the results obtained with any tissue extract. To obtain such an enormous dosage, moreover, would require fifty thousand calf glands (Christie, 1933). It does not seem possible, therefore, that he used only the carotid gland of the calf. This work, therefore, must also be discounted.

Removal of the carotid body causes temporary glycosuria in some animals (Vassali, 1910, quoted by Christie, 1933). Excision of the superior cervical ganglion is known to produce glycosuria (Lazioloth, 1915, quoted by Christie, 1933). It is quite possible that these investigators, in removing the

carotid body also removed a part of the superior cervical ganglion.

From these limited investigations no conclusive statement can be drawn regarding the glandular function of these bodies.

Summary

Pressoreceptors--characteristic nerve endings that respond to changes in pressure. In the lower vertebrates the regions responding to pressure changes are widespread. In the higher vertebrates they are confined to more definite regions.

1. Endings in the carotid sinus, from the third arch.
2. Endings on the right subclavian artery, from the fourth arch.
3. Endings on the arch of the aorta, from the fourth arch.

The physiology of the pressoreceptors is almost identical in the different forms studied. The glossopharyngeal and the aortic depressor nerves are the prime afferent nerves.

Chemoreceptors--characteristic nerve endings responding to changes in the respiratory gases. They increase in complexity up to the primates. In the primates and higher animals two different types of systems seem to exist.

1. Cat and Rabbit--small amount chromaffin cells
    - a. Carotid body, from the third arch.
    - b. Aortic bodies, from the fourth arch.
    - c. Paraganglion supracardiale, from the sixth arch.
2. Dog and Human--no chromaffin cells.
    - a. Carotid body, from the third arch.
    - b. Paraganglion supracardiale superius, from the fourth arch.

c. Paraganglion supracardiale inferius, from the fourth arch.

The nerve endings of the pressoreceptors and the chemoreceptors are identical. The only possible way of distinguishing them is by their relative positions. The chemoreceptors are located close to the endothelium of the capillaries or the arteries. They are usually associated with epithelioid cells. The pressoreceptors, on the other hand, are found in the adventitia or media of blood vessels.

Abstract

The literature reported in this paper indicates that the chemo- and pressoreceptors exist in all the vertebrates thus far investigated. The complexity of the different chemo- and pressoreceptors varies directly with the complexity of the form of the vertebrate studied. The histology of the different chemoreceptors is practically identical. The aortic depressor and the glossopharyngeal nerves are the afferent nerves.

The different pressoreceptors are also practically identical. The main afferent nerves involved are the sinus nerve of Hering and the aortic depressor nerve.

Much work has still to be done on the histology and embryology of these various structures before a comparative morphology, anywhere near adequate, can be compiled. Only the mammalia seem to have received much attention.

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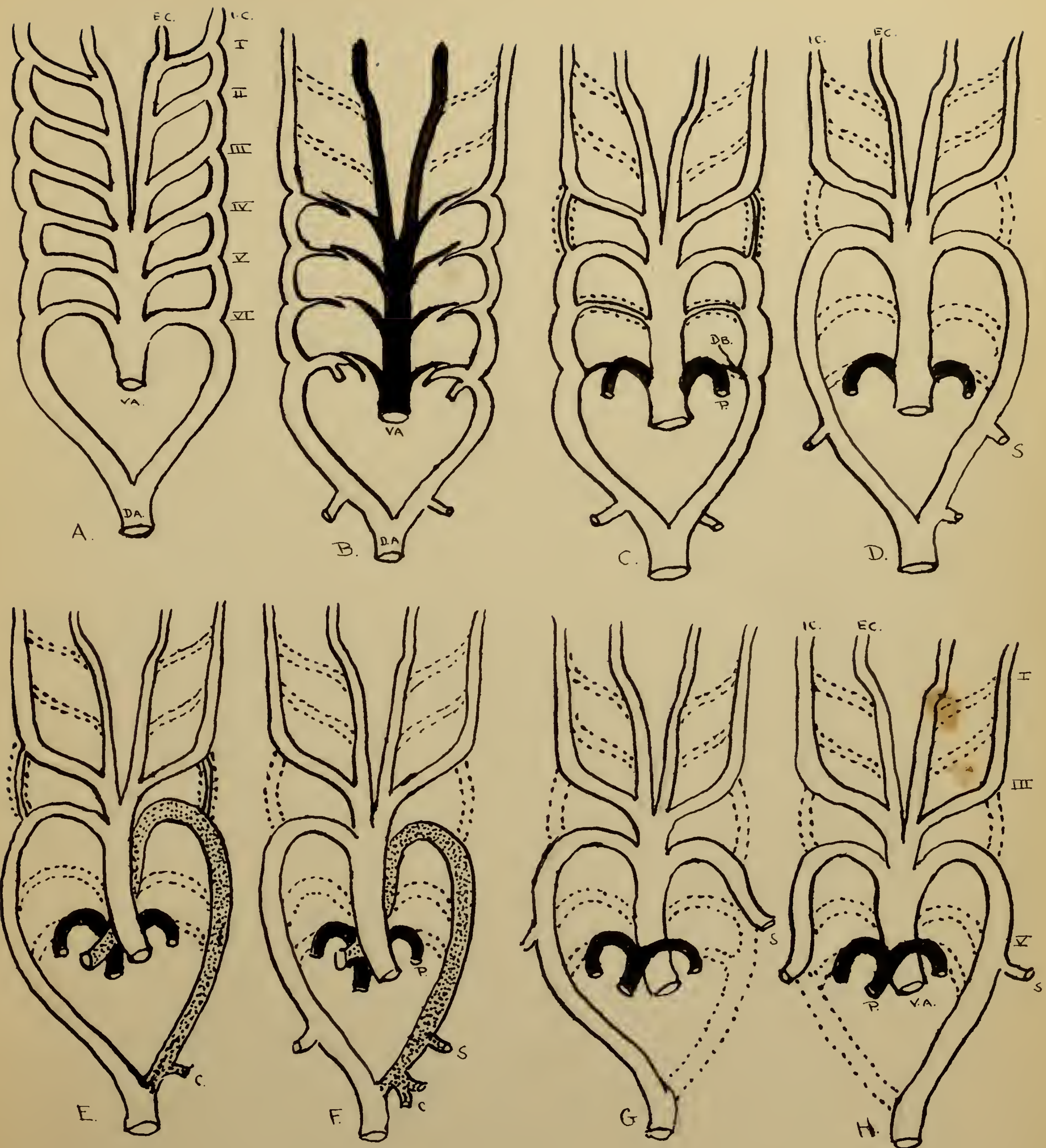
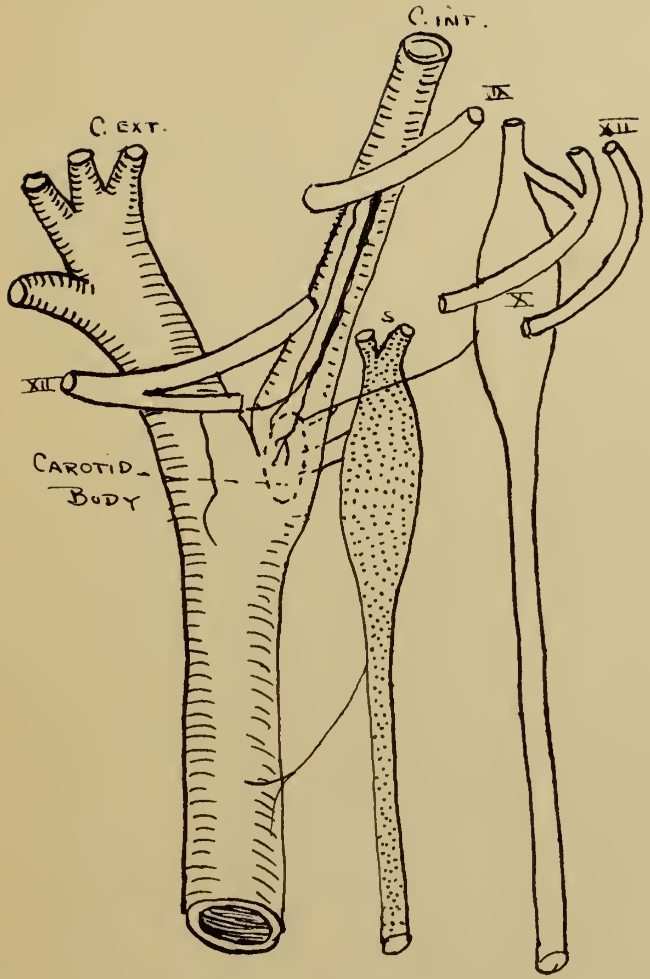


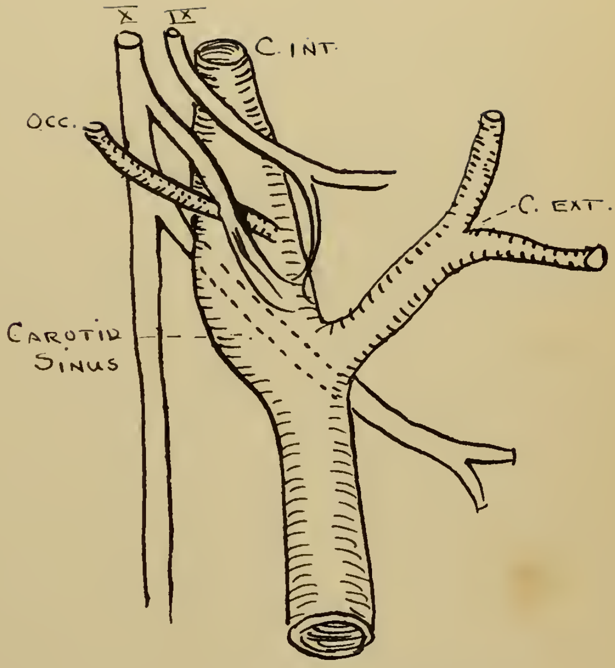
Modifications of the aortic arches in different vertebrates. A- Primitive Scheme; B: Dipnoian; C- Urodele; D= Frog; E- Snake; F- Lizard; G. Bird; H. Mammal.

C= Celiac artery; DA= Dorsal aorta; DB- Ductus Botalli; ec and ic External and internal carotid artery

Neal and Rand, 1936, pg.3



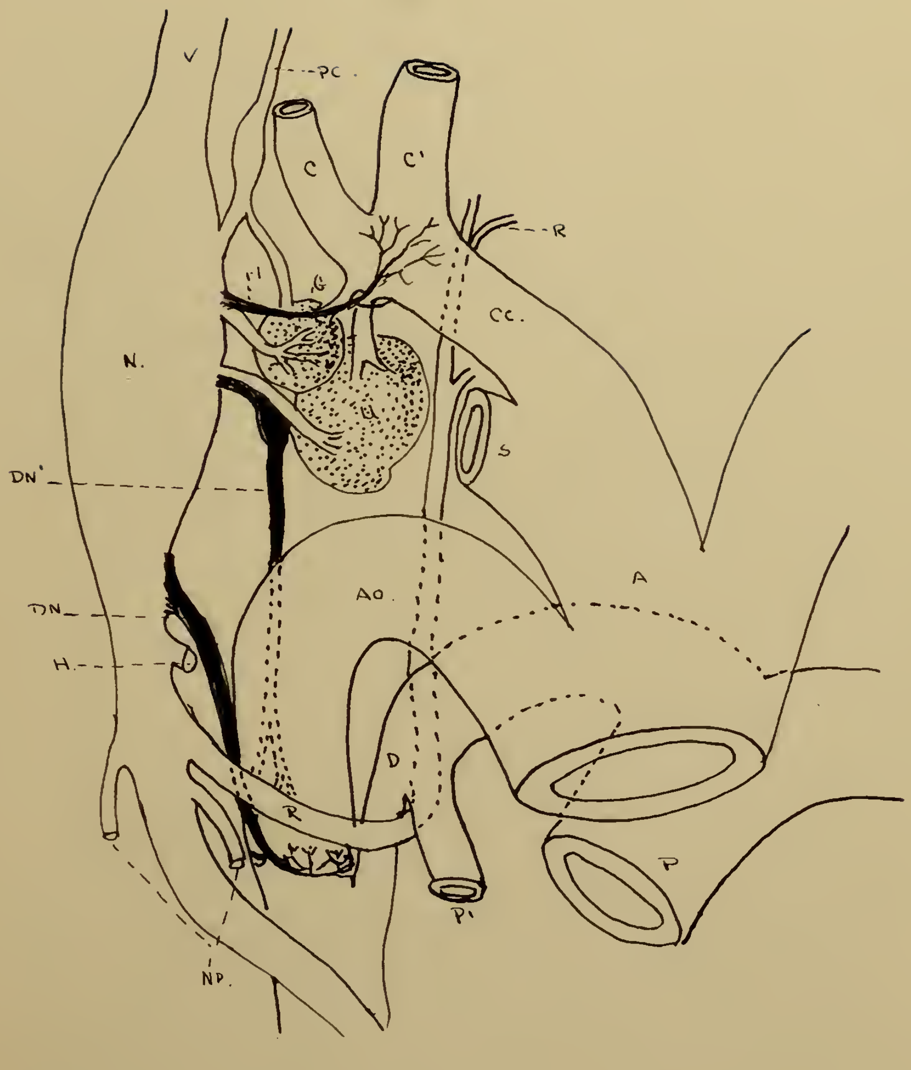
Sinus Innervation
in
Didelphs virginiana



Sinus Innervation
in
Erinaceus europoeus

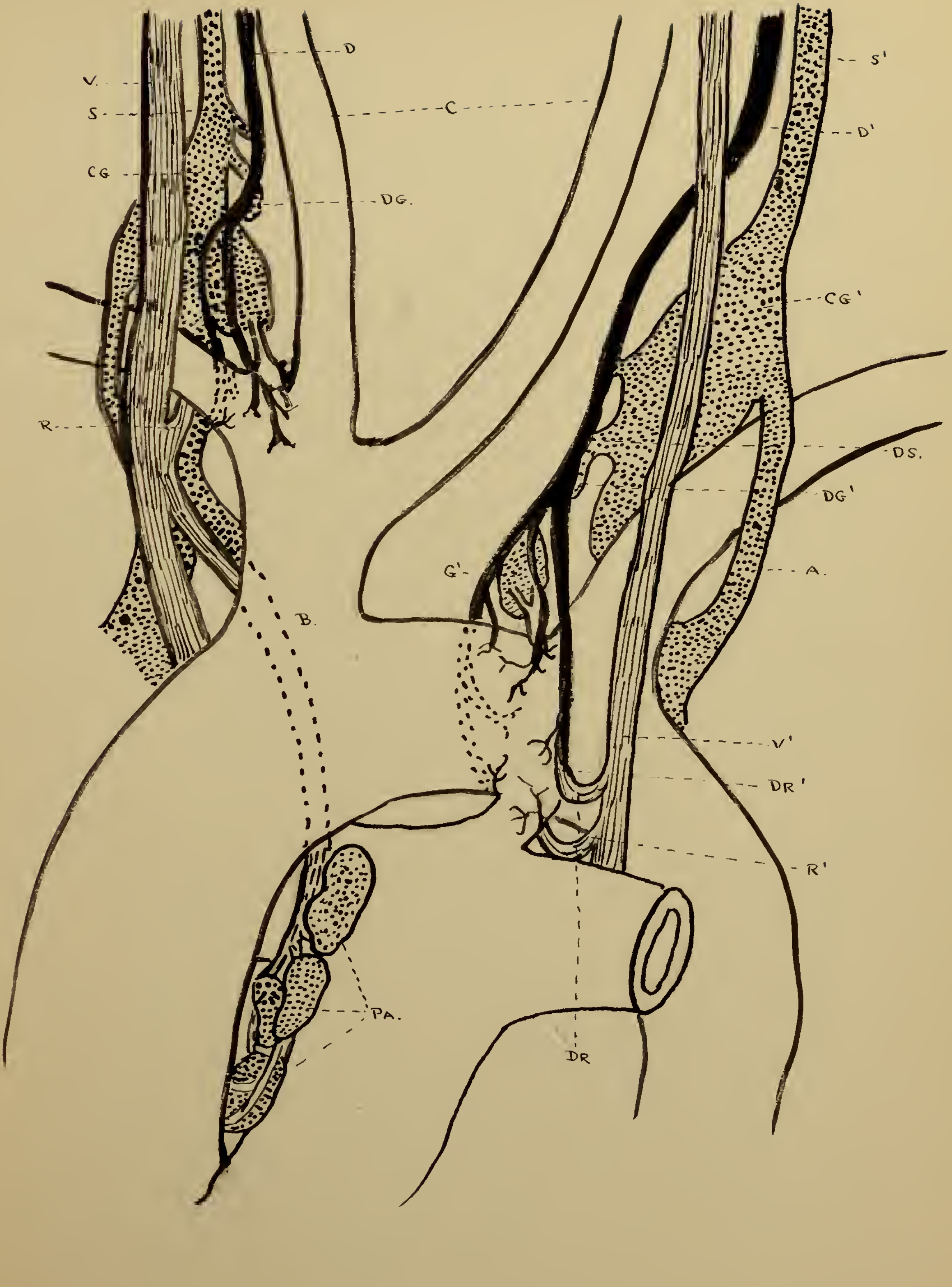
Ask Upmark, 1935, pg.

Diagram showing the pressoreceptors (in black) on the right side of the body of a newly hatched chick. Based on a reconstruction from transverse serial sections. (Chick III; alcohol ammonia fixation.) a, arteria anonyma (innominate); ao, aorta; cc, common carotid; c, c', internal and external carotids, respectively; d, ductus arteriosus; dn, depressor nerve; dn', accessory depressor nerve; g, glomus caroticum; h, cardiac nerve; i, depressor nerve of the carotid; n, ganglion nodosum of vagus; np, nerves to pulmonary plexus; p, pulmonary trunk; p', right pulmonary artery; pc, prevertebral precarotid trunk joining the ganglion nodosum and sending a branch to the glomus; r, recurrent nerve; s, subclavian artery; u, ultimobranchial body; v, vagus.



NUNIDEZ 1935, pg 50

Diagram showing the distribution of the aortic (depressor) nerves (d, d'), the position of the aortic glomi (g, g'), and the paraganglion aorticum supracardiale (pa). Based on a transverse series of a newborn rabbit. a, ansa subclavia; b, innominate artery; c, common carotids; cg, cg', inferior cervical ganglion; dg, dg', ganglion at the junction of sympathetic rami with the aortic nerve; dr, aortic branch of the vagus, with dr', its anastomosis with the ventral branch of the aortic nerve; ds, ramus of sympathetic joining the aortic nerve; r, r', recurrent nerve; s, s's, cervical sympathetic trunk; v, v', vagus.



Nonidez 1935 pp 260

Posterior view of the aorta and the pulmonary trunk. a", aortic fibers ending on the posterior surface of the arch of the aorta; ag, epithelioid cell group (right aortic glomus); cr, cardiac branch of the left recurrent nerve; g', g", superior and inferior groups of epithelioid bodies, respectively; ga, artery to superior epithelioid bodies. Other letters as in preceding figure.

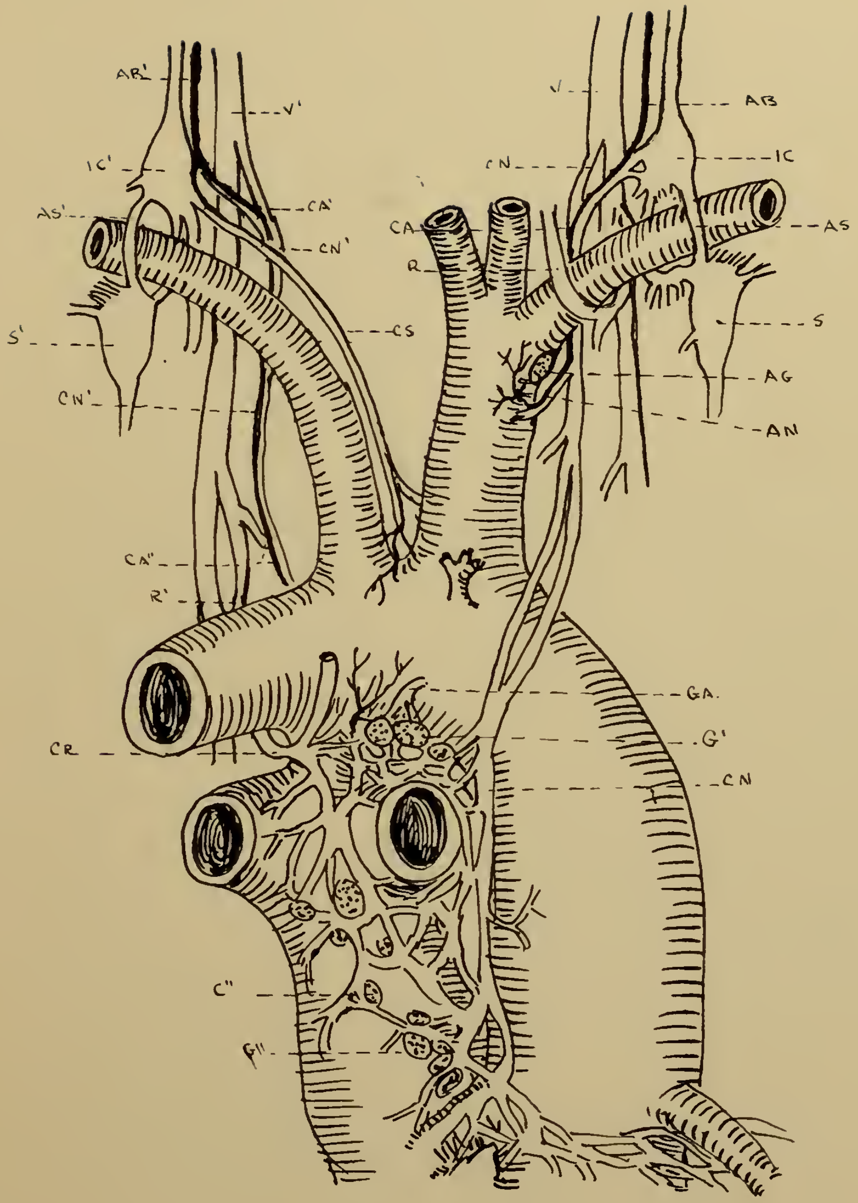

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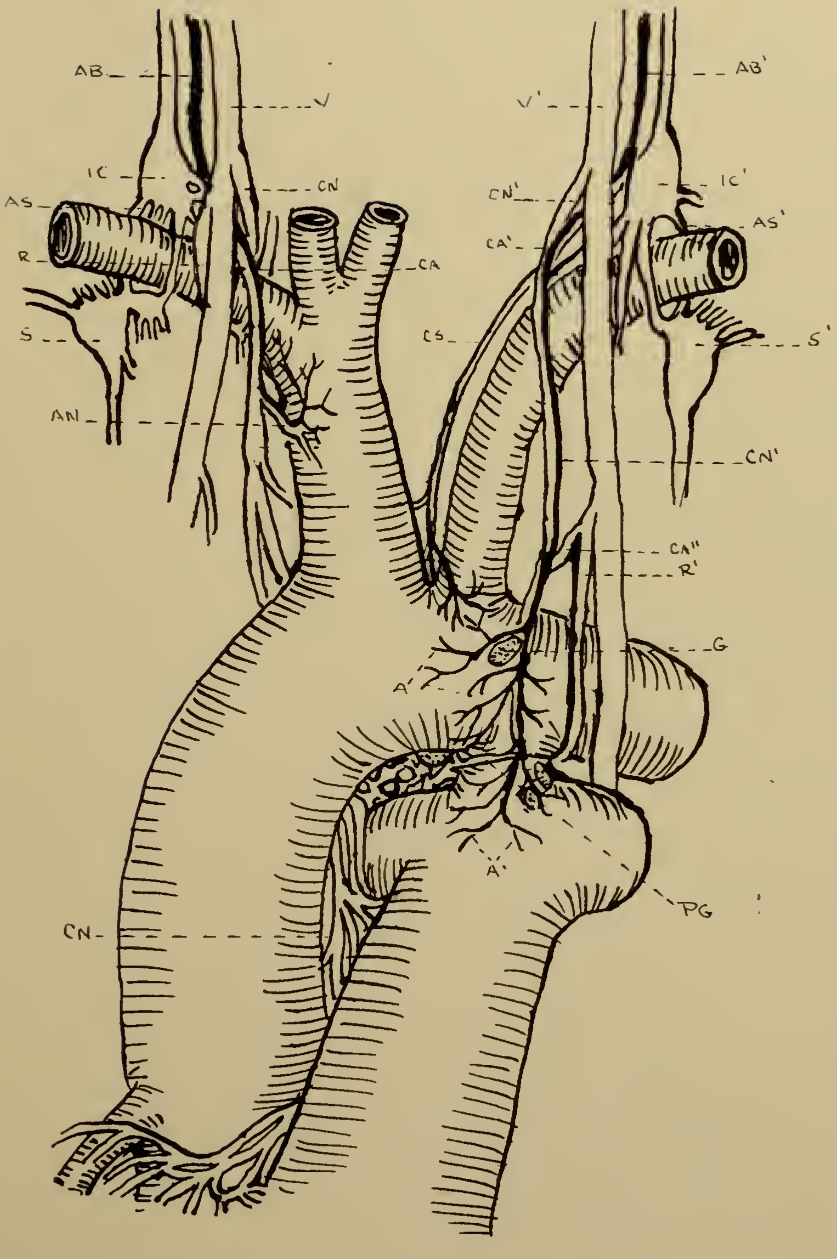
Diagram showing the distribution of the nerves bearing aortic fibers on the large arteries of the heart. Bundles of aortic fibers shown in black; epithelioid cell groups, stippled. One-day-old puppy. a, main pressoreceptor area; a', pressoreceptor area at the bifurcation of the pulmonary trunk; ab, ab', bundles of aortic fibers in the vago-sympathetic trunks; an, right aortic nerve; as, as', ansae subclaviae; ca, ca', anastomoses between the inferior cervical ganglia (ic, ic') and the cardiac nerves (cn, cn'); ca", anastomosis between the left cardiac nerve and the left recurrent, r'; cs, cardio-sympathetic nerve; g, epithelioid cell mass corresponding to the left aortic glomus; pg, bundle of preganglionics and fibers to the epithelioid bodies under the arch of the aorta; r, r', recurrent nerves; s, s', stellate ganglia; v, v', vagi.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